THE

AMERICAN NATURALIST.

VOL. XXXVII. *December, 1903.* NO. 444.

ADAPTATIONS TO AQUATIC, ARBOREAL, FOSSORIAL AND CURSORIAL HABITS IN MAMMALS.

III. FOSSORIAL ADAPTATIONS.

H. W. SHIMER.

THE purpose of the following article is to summarize a few of the principal modifications in external shape and in the skeleton independently acquired by mammals in different orders which have become wholly or partially adapted to a life beneath the surface of the ground. The highest specialization in this direction is found, as we should expect, in those forms which secure not only safety but also their food within the earth (*e. g.* the moles). Such forms are completely fossorial. On the other hand the procuring of food above ground and the use of the burrow merely as a safe place in which to live and rear young requires fewer fossorial modifications, and such forms may be called semi-fossorial, although, naturally, between fossorial and semi-fossorial no fixed line can be drawn. The following characters are best seen in the truly fossorial forms.

A. EXTERNAL MODIFICATIONS.

1. *Body more or less fusiform.*—An obvious adaptation to progression in such a dense medium as earth. In the common mole (Condylura), for example, the body-diameter is greatest at the shoulder, and diminishes gradually to a point at the nose. In some fossorial forms, *e. g.* the wombat (Phascolomys) and woodchuck (Arctomys), the body is very thick.

2. *Eyes imperfectly developed or obsolete.*—Normally developed eyes are traditionally useless to an animal living in complete darkness, and would be a continuous source of pain from injury received in burrowing. The degree of degeneration is no doubt partly dependent on the length of time which has elapsed since the assumption of fossorial habits, and on the relative completeness of withdrawal from the upper air. In the pocket gophers (Geomyidæ) and Bathyergidæ the eyes are small; in *Spalax typhlus* they are mere black specks among the muscles (although retaining a relatively complete structure); in the marsupial mole (*Notoryctes typhlops*) they are imperfectly developed and functionless; in Talpa they are vestigial; in the Cape golden mole (Chrysochloris) the eyes are covered with skin.

3. *External ears, small, tending to disappear.*—External ears impede burrowing especially as they are situated at the upper and anterior part of the body where much friction would naturally occur. Hence in the Geomyidæ and in Lutra the external ears are small, in the ratel (Mellivora) very minute and in the Bathyergidæ they have become reduced to a mere ring of skin around the auditory aperture, while in Notoryctes, Chrysochloris and Talpa they are absent.

4. *Limbs short and stout.*—Since in a truly fossorial animal strength to dig is of more importance than swiftness of progression on the surface of the ground the limbs are short and stout (Ornithorhynchus, Echidna, Talpa, etc.). This of course does not hold good for the majority of semi-fossorial forms, as in their life above ground they need speed either to get food or to escape enemies. Many of these, however, as our common wood-

chuck (*Arctomys monax*) and the wombat (Phascolomys), have legs quite short and stout; while for example in the pig-footed bandicoot (*Chœropus castanotis*) the legs are long and cursorial in type. In the latter animal the external ears are also very long.

5. *Manus broad and stout, with long claws.*— The fore feet and hind feet have undergone divergent specialization, since the fore feet are used to loosen the earth, while the hind ones merely throw it further backward. Hence the manus becomes broad and stout with very strong claws. In the common mole (Condylura) the manus is as broad as the whole body, and hence it can dig with exceeding rapidity, excavating with one sweep of the arm a place wide enough for entrance. In Echidna also the manus is broad. The enlarged strong claws are well seen in Notoryctes, Phascolomys, Taxidea and the Geomyidæ.

6. *Pes modified to throw the loose earth backward.*— The pes has the claws well developed although not nearly so strongly as in the manus. Some animals have developed special adaptations for throwing back the loose earth. In Phascolomys the second, third, and fourth digits are partly connected by skin. This web is of course strongly developed in such swimming forms as Chironectes and Scalops but it is also a great aid to them in burrowing. Heterocephalus has the feet fringed with stiff hairs, while the Octodontidæ have long stiff hairs at the roots of the claws. The hallux is at times vestigial as in Phascolomys.

7. *Tail usually short.*— A tail seems to be a useless appendage to an animal surrounded closely by earth so it becomes quite short even in many semi-fossorial forms as in the hare, ratel, and woodchuck. In the wombat, moles, etc., it is vestigial. Oryzoryctes is an exception, for although fossorial it has a comparatively long tail.

B. Skeletal Modifications.

1. *Skull in top view triangular, apex forward.*— The subconic form of the skull is one of the obvious adaptations to progression through a dense medium. It is very well seen in Condylura, *Crossopus fodiens*, etc.

2. *Zygomatic arches not extended outside the greatest width of the skull.*— All projections from the usual regularly shaped skull become reduced. The zygomatic arches are very slender (*e. g.* Condylura, Talpa, Erinaceus, Orycteropus).

3. *Prenasal ossicle.*— A small prenasal ossicle is developed at the tip of the mesethmoid cartilage in Talpa as it is in the pig (Sus), due doubtless to the same cause, that of using the nose as an aid in digging.

4. *Incisor teeth chisel-shaped, projecting forward.*— In some forms the large incisors serve to keep earth out of the mouth, in others they are used as an aid in digging. The wombat (Phascolomys) for example has a pair of strong chisel-shaped projecting lower incisors. Among the rodents *Spalax typhlus* for example has the well developed lower incisors projecting beyond the lower jaw; the bamboo rat (Rhizomys) uses its incisors to aid in digging, in the Bathyergidæ the entrance of earth is prevented by the upper incisors which extend in front of the closed lips.

5. *Cervical and lumbar vertebræ more or less fused.*— The fusion of these vertebræ gives strength and firmness in pushing (*e. g.* Notoryctes and the armadillos). It is possible that the peculiar intercentral ossicles observed below the lumbar vertebræ especially in Talpa and the Erinaceidæ may be of use in strengthening the spinal column. Phascolomys and the Dasypodidæ have the cervical vertebræ wide and depressed; in the latter several of them are commonly anchylosed. In Talpa, the fourth, fifth and sixth cervicals are much lengthened and overlap each other.

6. *Transverse processes of lumbar vertebræ very short.*— Since in truly fossorial forms there is but little up and down or from side to side movement in the lumbar region, the corresponding muscles and their attachments, the transverse processes are feebly developed (*e. g.* Erinaceus).

7. *Sacrals fused.*— The main stress in pushing comes on the sacrals; in the majority of fossorial forms (*e. g.* Condylura, Lepus) they fuse even to a greater extent than in cursorial animals, as no lateral or vertical displacements but only rigidity are required of them.

8. *Sternum well developed.*— The anterior part of the trunk requires rigidity, great strength and ample surfaces for the attachment of the hypertrophied digging muscles. The individual bones tend to become short and broad and the processes for muscular attachment prominent (*e. g.* armadillos). In the moles change of position of the fore limb is correlated not only with the broadening but especially with the elongation of the presternum; at the same time the clavicle is extremely broad, and shortened so that the limbs may project as little as possible from the sides of the body; the limbs are but slightly shortened, so that the leverage of the muscles is unaffected. In Chrysochloris this need is met by the invagination, as it were, of the walls of the thorax for the reception of the arms, the ribs and sternum being convex inward. The clavicle is usually, as in Chrysochloris, curved backward from the sternum, so that the shoulder may slope gradually forward and not be an angular projection interfering with progress through the earth.

9. *Bones of fore limb strong, tuberosities prominent.*— The fore limbs being the principal organs for digging are well developed, while the tuberosities, ridges, etc., for the insertion of muscles are very prominent. Sesamoid bones are frequently developed in the palms, as in Echidna where also the breadth of the hand is increased by a radial sesamoid (os falciforme of Talpa). The humerus is usually stout and broad as in Talpa, Phascolomys, Echidna, etc., with prominent deltoid and supinator ridges. These are carried to an extreme in Talpa where the deltoid ridge joins the inner tuberosity above. The olecranon process is always strongly developed. A supracondylar foramen is usually present.

10. *Ilium and ischium rod-like, parallel to the vertebral column and fused to the sacrum.*— The hind limbs being mainly used for pushing the body through the earth, their point of attachment to the body must be firm and they must deliver the forward thrust in a more or less horizontal plane. So we find that the ilium is long and fused usually throughout its entire length to the vertebral column; this is especially true of the moles.

11. *Bones of hind limb not so strongly developed as those of fore limb.*— Besides pushing the body forward the hind limbs

are principally used for throwing back the loose earth. Although not acquiring the excessive development of the fore limbs, the femur usually has its trochanters well developed. In Erinaceus it has a strong ridge below the third trochanter. Greater strength is given by the partial anchylosis of the tibia and fibula; in Chrysochloris they are welded at the lower end. Strength is effected in the pes by the great development of the calcaneum, which plays a prominent part in pushing the animal forward. In Talpa the pes has a large sesamoid bone at the side of the tibia corresponding to the os falciforme of the manus, but otherwise it exhibits none of the great modifications of the manus.

C. Physiological Modifications.

1. *Hibernation.*— In the temperate zones where the ground is frozen during a portion of each year, fossorial mammals would have difficulty in getting food. Especially is this the case with those semi-fossorial forms such as the woodchuck which live on soft succulent herbage. Such forms are thus compelled to spend the winter in a long sleep (*e. g.* woodchucks, gophers, hamsters, etc.).

Partial List of Fossorial and Semi-fossorial Mammals.

Monotremata: Ornithorhynchus, Echidna; Marsupialia: Phascolomys, Dasyurus, kangaroo rat, *Bettongia leseuiri*, pig-footed bandicoot (*Chœropus castanotis*), marsupial mole (*Notoryctes typhlops*); Edentata: Dasypodidæ, Orycteropus; Insectivora: Talpa, Condylura, Scalops, water shrew (*Crossopus fodiens*), desman (Myogale), Erinaceus, Oryzoryctes, Chrysochloris; Rodentia: Lepus, Spermophilus, Cynomys, Arctomys, Geomyidæ, Spalacidæ, Rhizomys, Octodontidæ, Cœlogenys, Viscacha (*Lagostomus trichodactylus*), Bathyergidæ, Heterocephalus; Carnivora: Lutra, ratel (Mellivora), Javanese skunk (Mydaus), American badger (Taxidea).

The anatomical conditions prerequisite to progressive modification along fossorial lines evidently include the following: reten-

tion of the primitive characters of small size, generalized (*i. e.* short, more or less plantigrade, pentadactyl) limbs with moderately sized claws and normal relations of the radius and ulna, clavicle and muscles used in digging unreduced, face pointed elongate, dentition adapted to food found in the earth. Hence it is natural that the majority of fossorial forms should have sprung from primitive and defenceless rodents, insectivores and edentates and that the carnivores (especially those with specialized sectorial dentition) the ungulates (mostly herbivorous, and cursorial), the primates (typically light limbed, light clawed, short faced), have as a rule failed either to find protection from foes or abundant food by turning into the barred road of fossorial modification.

BIBLIOGRAPHY.

BEDDARD, F. E.
:**02**. Mammalia. Cambridge Nat. Hist. Vol. 10.
FLOWER, W. H. and LYDEKKER, R.
'**91**. An Introduction to the Study of the Mammals Living and Extinct.